LAMELLIBRACHIA BARHAMI, GEN. NOV., SP. NOV. (POGONOPHORA), FROM THE NORTHEAST PACIFIC

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ABSTRACT

Lamellibrachia barhami, gen. nov., sp. nov., is a large and unique pogonophore which has been assigned to the Afrenulata, class nov.; order Vestimentifera, order nov.; and family Lamellibrachiidae, fam. nov. All previously known Pogonophora are included in a new class, the Frenulata, class nov. The fundamental distinction between the two classes lies in the presence or absence of a bridle (frenulum). The tentacular crown is formed of numerous, fused, horseshoe-shaped tentacle lamellae arranged concentrically around a central paired lophophoral organ. The second segment is characterized by two body folds meeting midventrally and enclosing a vestimental tube in which lie two ciliated grooves, at the posterior ends of which open the male and female genital ducts. The trunk, comprising 89 per cent of the total body length, is undifferentiated. The terminal body region, the true metasoma, is without setae. There is a pair of simple ciliated excretory ducts opening by a common excretory pore into a ventral groove at the base of the tentacular crown. The heart is a simple muscular elaboration of the anterior end of the ventral blood vessel. The second, or vestimental region, is without coelomic cavities for most of its length; however, the paired coelomic cavities of the trunk project into the posterior end of the vestimental region. The brain is large, and from it arises a pair of intra-epidermal nerve cords which extend the full length of the vestimental region; thereafter they join and form the median intra-epidermal nerve cord of the trunk. Associated with the brain and the nerve cords are the characteristic dorsal tubes.

INTRODUCTION

Specimens of **Lamellibrachia barhami,** gen. nov., sp. nov. were collected at a depth of 1125 m with the "arm" of Deepstar 400 on dive 196 by Dr. Eric Barham of the U. S. Navy Electronics Laboratory, San Diego, California. Dr. Barham in a personal communication provides the following valuable information: "The tangle of tubes were entwined and sitting completely exposed on a 45° silty slope, but next to and partially surrounded by large boulders and outcrops. When first seen their red lophophores were fully exposed but these were contracted rapidly in the manner of sabellid tube worms." The temperature at depth of collection was about 3.0°C and salinity about 34.5‰.

The purpose of this work is to describe the main features of the animal, including such brief references to internal organization as are necessary in order to establish it within the phylum Pogonophora. Fuller and more detailed anatomical accounts are in preparation and will be published from

TABLE 1

MEASUREMENTS, IN MILLIMETERS, OF TUBES OF FOUR SPECIMENS OF *Lamellibrachia barhami*

Tube	Length of tube	Diameter of tube	
		Maximum	Minimum
A	610	7.3	1.0
B	641	9.0	2.1
C	599	8.9	1.0
D	724	7.0	0.9
Average	644	8.05	1.25

time to time so as to provide a clear picture of the animal. When this is complete, a detailed discussion will be given as to the possible inter- and intraphyletic relationships.

Holotype.—The specimen was collected by Dr. Eric Barham from the type-locality on 17 December, 1966. Reduced to a series of slides, the holotype will be deposited in the U. S. National Museum.

Type-locality.—Northeastern Pacific, 32°19.6′N; 117°19.08′W.

Other Specimens.—Of the seven other specimens, one will be deposited in the U. S. National Museum, one will be deposited in the British Museum (Natural History), and the rest are deposited in the Zoology Department, University College, Durban, South Africa, with the number UCDZ 67:2.

ABBREVIATIONS USED IN FIGURES

b, brain
bc, brain cover
c, coelom
cbv, cerebral blood vessel
dbv, dorsal blood vessel
dll, dorsolateral line
dm, dorsal mesentery
dt, dorsal tube
ed, excretory duct
eo, excretory organ
h, heart
imtl, inner mass of tentacular lamellae
l, lophophore (base of crown)
lc, lophophoral cupule
ldnc, left dorsal nerve cord
ldt, left dorsal tube
lm, longitudinal muscles
lo, lophophoral organ
lobv, lophophoral blood vessel
loc, coelom of lophophoral organ
lov, left ovary
mdl, median dorsal line
ob, opisthomere bulb
os, ovisac
otl, outer tentacular lamella
rov, right ovary
t, testis
tbv, tentacular blood vessel
tc, tentacular crown
tl, tentacular lamellae
tr, trunk
vbv, ventral blood vessel
vc, vestimental collar
veg, ventral excretory groove
vfl, left vestimental fold
vfr, right vestimental fold
vg, vestimental groove
vt, vestimental tube

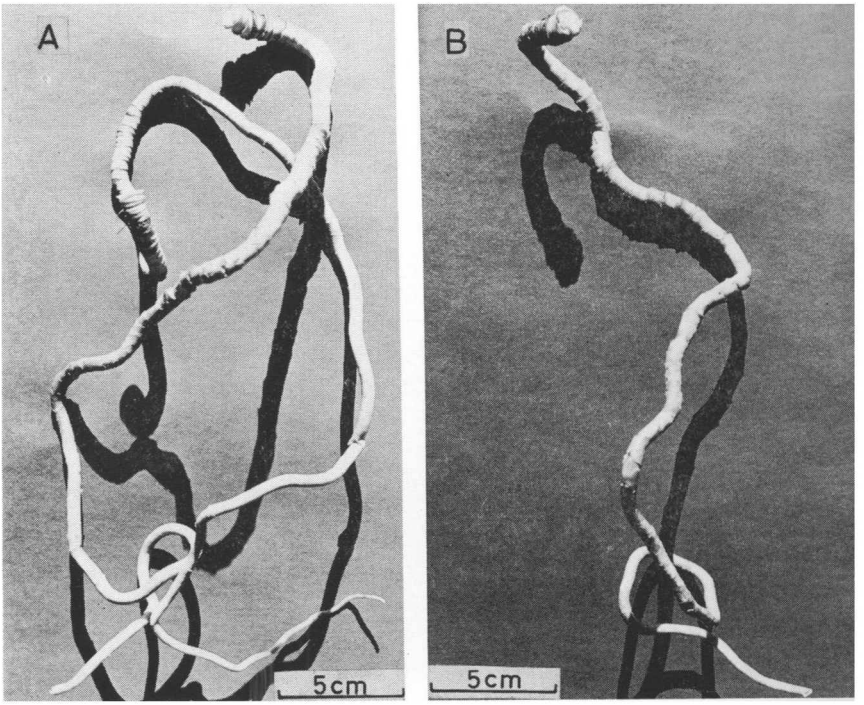

FIGURE 1. A, B, photographs of complete tubes of two specimens.

THE TUBE

Three of the four tubes (A, B, and C) studied were complete; on the fourth tube (D), only the extreme anterior collared end was missing. The measurements of all four tubes are tabulated below (Table 1).

The tubes are unsegmented, bent, and twisted (Fig. 1,A,B). For most of their length they are very hard and inflexible with only the narrow posterior end being slightly flexible. Each tube tapers from a broad funnel-shaped anterior end to a narrow posterior end.

The colour of the tube is difficult to describe, but for purposes of the record the anterior collared end is whitish cream with black/brown markings; the middle portion of the tube is pale brown and, because of the enclosed animal, it has an olive-green tinge; the short posterior end of the tube could be described as being straw coloured.

A feature of the tube is that it can be roughly divided into three regions. There is a short anterior region characterized by irregularly spaced, more or less transverse ridges (or collars, preferably called funnel rims, a point to be discussed later). Such ridges gradually diminish in size from the

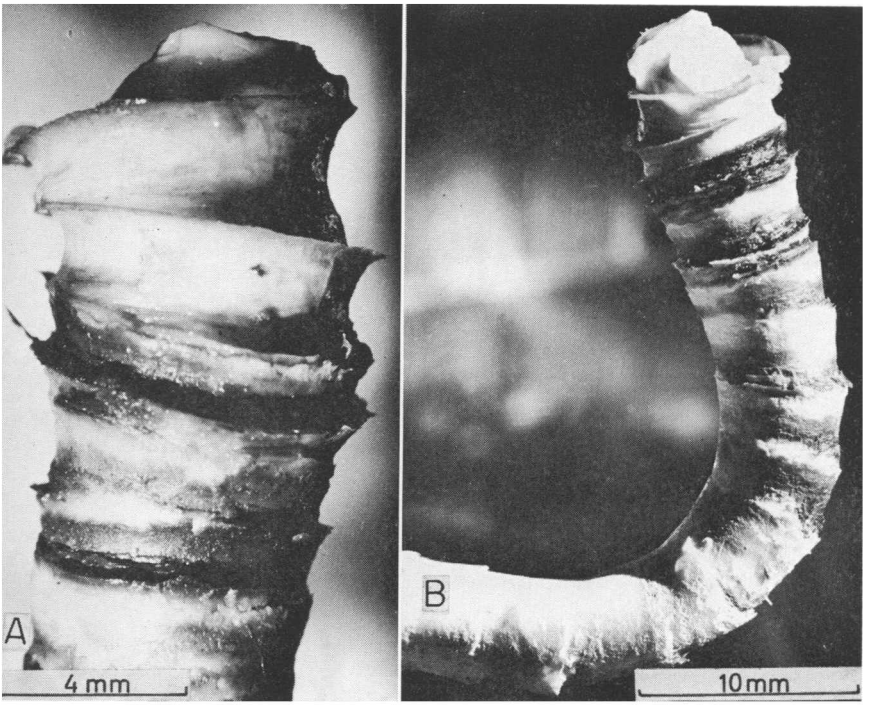

FIGURE 2. A, B, enlargements of the anterior end of the tube, from two angles.

funnel-like opening until they are no longer distinguishable (Figs. 1, 2, and 3,A,B).

Immediately posterior to the short collared region is a second region comprising most of the tube's length, showing transverse, or transverse-oblique lines which are irregular and somewhat tattered in appearance (Fig. 3,A). Further posteriorly there is no regular pattern for the lines; they are irregularly spaced, transverse or oblique, and the edges are also irregular (Fig. 3,B). These irregular lines represent the remains of the bases of earlier terminal funnels which have broken down through a flaking off of the outer layers of the laminated tube.

The last region of the tube is short, has a smooth surface without lines or ridges, and opens to the exterior by a small terminal pore (Fig. 3,C).

Other features of the tube came to light when the animals were removed. In order to remove the animals, the tube was shaved with a sharp scalpel along its length. It was found that the superficial layers were easily removed by peeling them off; the flakes were very hard and brittle. Beneath these superficial layers there was a fairly thick layer, of glassy appearance,

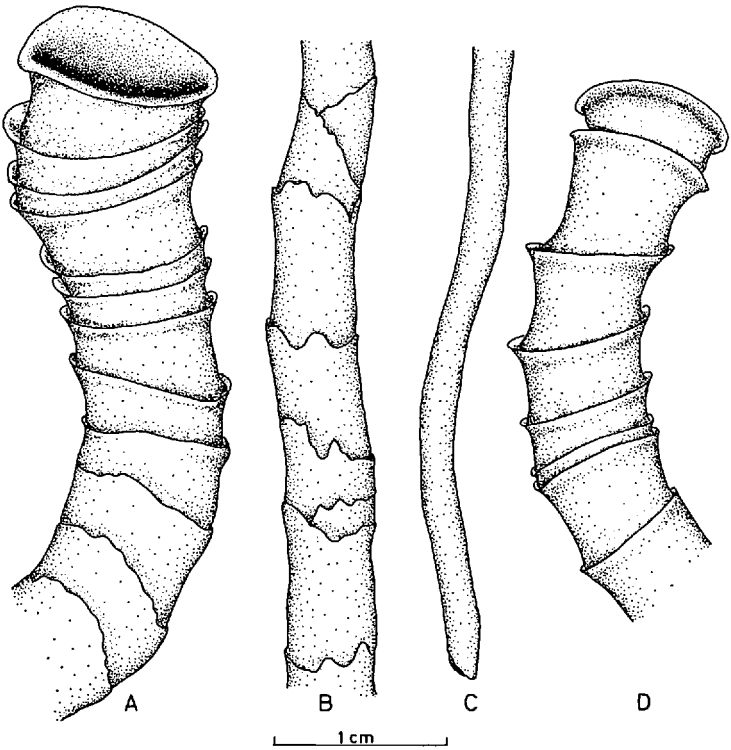

FIGURE 3.—A-C, portions of a single tube of *Lamellibrachia barhami*: A, the anterior end; B, a piece from the middle of the tube; C, the posterior end.—D, the anterior end of a second tube.

which to the unaided eye appeared to be homogenous. This layer, however, also proved to be composed of compacted layers of material which could be stripped off layer by layer. The innermost layer was exceedingly thin and tended to adhere to the body of the animal. In attempting to remove it, partial damage to the animal resulted.

Discussion.—The tube of this species is one of the longest on record. Its length is exceeded only by the length of the tube of *Zenkevitchiana longissima* (Ivanov, 1957, 1963), which is 1500 mm, or about twice as long. The tube of *Polybrachia annulata* (Ivanov, 1952, 1954, 1963) is 500-600 mm long, and that of *Galathealinum arcticum* (Southward, 1962: 385) is 340-500 mm, "but still incomplete." It seems reasonable to assume that there may be many other pogonophoran species that will prove to have considerably longer tubes, once we are able to obtain complete tubes.

TABLE 2

CHARACTERISTICS OF THE ANTERIOR END OF THE TUBE OF SOME MULTITENTACLED POGONOPHORA

	Collared	Flimsy	Saucered	Funnel-like
Galathealinum bruuni	+	?[1]	0	0
G. brachiosum	+	?[1]	0	0
G. arcticum	+	?[1]	0	0
Heptabrachia celebensis[2]	+	+	0	0
Diplobrachia capillaris[3]	+	?[1]	0	0
Polybrachia annulata	+	?	?	?
P. gorbunovi	+	0	+	+
Choanophorus indicus	+	?	+	?
Lamellisabella johanssoni	+	0	+	+
L. minuta	+	0	+	+
Spirobrachia grandis	0	0	0	+
Lamellibrachia barhami	+	0	+	+

[1] No information provided.
[2] Of the eight species of *Heptabrachia*, five have tubes with collapsed, flimsy, transparent anterior ends. In *H. berengensis* (Ivanov, 1963) the tubes are incomplete; in *H. canadensis* (Ivanov, 1962) the front and hind ends of the tubes are broken off; and for *H. talboti* (Southward, 1961a) no information is given other than that the longest tube is incomplete. It can be assumed that all the species of *Heptabrachia* have a collapsed anterior end to the tube.
[3] Of the four species of *Diplobrachia* (i.e., *japonica, southwardae, belajevi,* and *capillaris*) (Ivanov, 1963), the tubes of the former two have a flimsy, transparent, collapsed anterior end. For the latter two no information is provided, but it could be that such a flimsy end is in reality present but has been lost during collection, for Ivanov (1963) described *D. belajevi* from 14 small pieces of tubes, four with incomplete animals.

Though there are possibly many more pogonophoran species with tubes of comparable length and longer, there are no records of species with a maximum diameter of tube approaching that of this new species, which ranges from 7.0 mm to 9.0 mm. The largest diameter on record is 3.0 mm for a single specimen of *Spirobrachia grandis* (Ivanov, 1952, 1954, 1963), with the next largest being 2.8 mm for another specimen of *Spirobrachia grandis*. The tube of *Galathealinum brachiosum* (Ivanov, 1963) has a maximum diameter of 2.6 mm. Thus the tube of this new species has a diameter some 2.5 to 3 times greater than the diameters recorded for the hitherto described pogonophoran species.

The structure of the tube is similar to that of other pogonophoran tubes in the possession of collars along part of the anterior end of the tube, and also in the possession of an anterior funnel-like opening. There are ten pogonophoran species belonging to six genera having collared tubes. It is possible to divide these into two groups, basing such a division on the nature of the collar and the anterior opening (Table 2). It is noticed that in those species whose tubes have a flimsy, transparent, collapsed anterior section, the portion of the tube immediately behind this is not formed of what has been described as a "pile of saucers," while those species whose tubes do not have a flimsy and collapsed portion do have the anterior

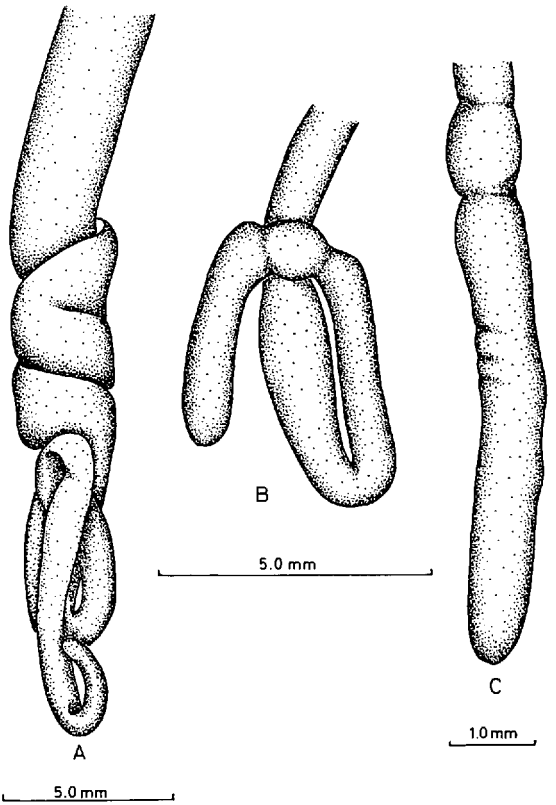

FIGURE 4. A, the opisthomere and coiled posterior end of the trunk of one specimen; B, C, the opisthomere and a small portion of the trunk of two further specimens illustrating the bulbous region with pre- and post-bulb constrictions.

"segments" arranged as a "pile of saucers," and also have a funnel-like opening to the tube. It is to the second group that this new species belongs.

In the first group, i.e., the nonsaucered tube (possibly excluding the genus *Galathealinum*), it appears that after a new tube segment is added in order to lengthen the tube, a new, anterior, flimsy portion of tube is added in front of the new segment, and that the old collapsed portion breaks down, leaving only a basal remnant that will ultimately disappear. This seems to explain why only the anterior part of the tube has such frilly collars, and then only at the anterior end of each segment.

In the second group, i.e., the saucered tube, with an anterior funnel-like opening (with the possible exclusion of *Polybrachia annulata*, Ivanov, 1952,

1954, 1963), the animal adds new portions to the tube, regularly or irregularly, possibly as a result of environmental fluctuations. Such new additions always end in a splayed funnel-like opening, thereby giving to the tube the characteristic appearance of a "pile of saucers." In the majority of saucered tubes the oldest portion is without collars. This suggests that the original rims of the funnels break down by a process of fragmentation until all signs of the original rims have disappeared except for the irregular lines so often to be seen on pogonophoran tubes well back from the anterior end.

The Animal

The terminology used in giving the description of *Lamellibrachia barhami* is that suggested by Webb (1964a-e, 1965) for the adult body regions of Pogonophora. The author is convinced that the interpretation of these regions by Ivanov (e.g., 1963, 1964) is incorrect, because it was based on incomplete animals. A paper dealing with this problem is in preparation and will be published shortly.

This description is based on the external morphology and some anatomical features of three specimens—one female and two males. The range in total length of specimens is from 369 mm to more than 426 mm (average 396 mm). Except for one specimen, the length given exceeds the measurements recorded, because the extreme posterior end of the trunk was coiled (Fig. 4,A) and it was, as a result, impossible to measure without damaging it. The maximum average diameter is 5.50 mm, and the minimum average diameter, 0.76 mm. Table 3 gives a comparison of the measurements of the three animals.

For purposes of this description, the body is divided into four clearly defined regions. After each region is given, in parentheses, the terminology of the divisions of the adult body, first as proposed by Webb (1964e) and second as given by Ivanov (e.g., 1963, 1964). The regions are: the *tentacular crown* (protosoma; protosoma); the *vestimental region* (agonadal mesosoma; mesosoma); the *trunk* (gonadal mesosoma; metasoma); and the *opisthomere* (metasoma; metasoma).

External Morphology

The Tentacular Crown.—There is no protosomal cephalic crown. The tentacular crown is paired, with the halves closely applied to each other when the animal is withdrawn into the tube. Proximally, the crown is protected by an anterior collar-like extension of the second, or vestimental region (Figs. 5; 6; 7,A; 9,A,B).

The crown is formed from three distinct parts. Externally there are two pairs of free tentacular lamellae, followed by a middle mass of some 25

TABLE 3

REGIONAL MEASUREMENTS, IN MILLIMETERS, OF THE BODIES OF THREE SPECIMENS OF *Lamellibrachia barhami*

Specimen	Total length	Length of tentacular crown[1]	Vestimental region		Trunk			Opisthomere		
					Diameter					
			Length	Diameter	Maximum	Minimum	Length	Length	Diameter	Diameter of bulb
A	369	9.0	25.4	4.8	4.5	0.70	329.34 (89%)	5.26	0.79	0.83
B	+426[2]	4.5	35.0	6.0[3]	4.5	0.72	382.3[2] (89.6%)	4.2	0.90	1.10
D	+392[2]	9.4	30.3	4.7	4.7	0.80	349.3[2] (89%)	3.0	0.58	?
Average	+395.6	7.63	30.23	5.5	4.5	0.71	353.6 (89%)	4.15	0.76	0.965

[1] That part of the lophophore lying outside the vestimental collar.
[2] Posterior end of trunk coiled.
[3] Vestimental folds slightly open.

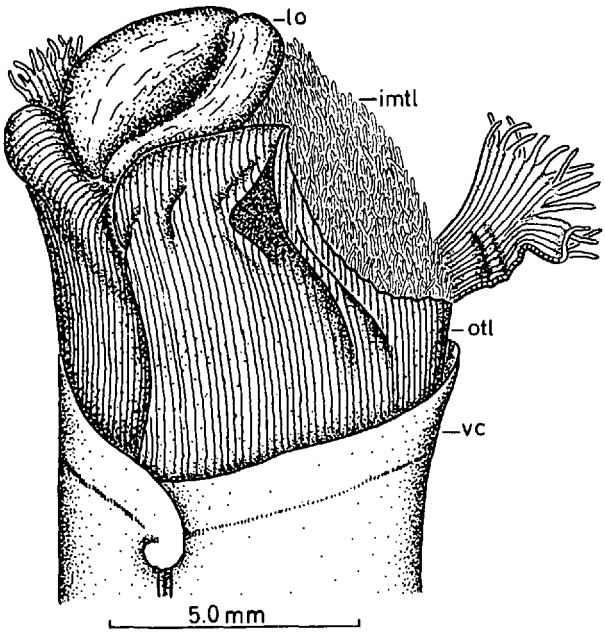

FIGURE 5. Dorsal aspect of the tentacular crown and vestimental collar, illustrating the outer tentacular lamellae, the inner mass of tentacular lamellae (shown only as the short, distal, free tentacles), and the distal end of the lophophoral organ in the form of a cupule.

fused tentacular lamellae arranged in a horseshoe around an inner paired structure, here called the lophophoral organ (Figs. 5; 6; 7,B).

The outer two pairs of tentacular lamellae are dorsolateral, and ventrolateral in position. They are free from one another and free from the mass of fused tentacular lamellae. The members of one pair overlap each other middorsally; the members of the other pair overlap midventrally. Laterally, the dorsolateral pair overlaps the ventrolateral pair. Both pairs arise from the base of the crown (lophophore proper), and each is formed from numerous fused tentacles. Distally each lamella is fringed with short free tentacles corresponding in number with the number of tentacles forming each lamella (Fig. 5).

The mass of tentacular lamellae arises from the crown base (or lophophore proper) and is arranged concentrically around the centrally placed lophophoral organ (Fig. 7,B). The mass appears to be horseshoe-shaped with the free edges of the arms meeting in the midventral line. Each lamella is formed from numerous fused tentacles and each lamella has a distal fringe of short free tentacles equal in number to the number of

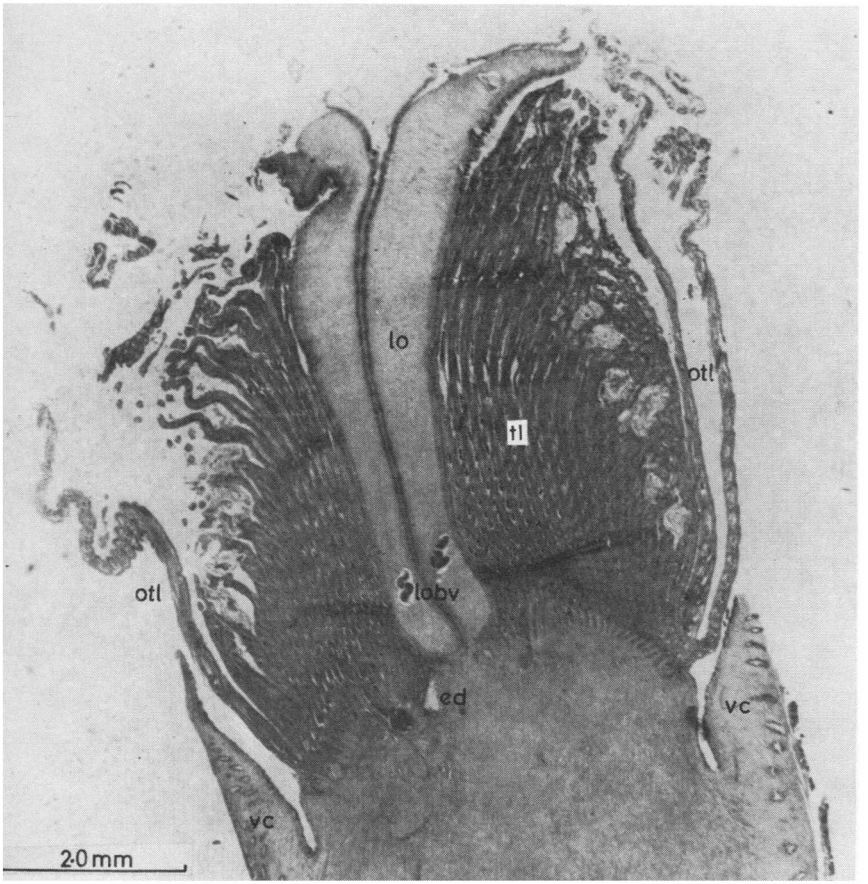

FIGURE 6. Photomicrograph of a horizontal longitudinal section through the tentacular crown and anterior end of the vestimental region.

tentacles forming the lamella. Further, it appears that all the lamellae are fused with one another (Figs. 5,B; 6). Additional tentacular lamellae probably develop throughout the life of the animal and these arise between the lophophoral organ and the innermost lamella.

The total number of lamellae forming the crown is about 25, and the average number of tentacles per lamella is about 80, which means that there are about 2000 tentacles forming the crown.

The third, and possibly the most distinctive, part of the tentacular crown is the paired lophophoral organ which forms a central core and supporting structure around which the lamellae are arranged (Figs. 5; 6; 7,A-D; 8).

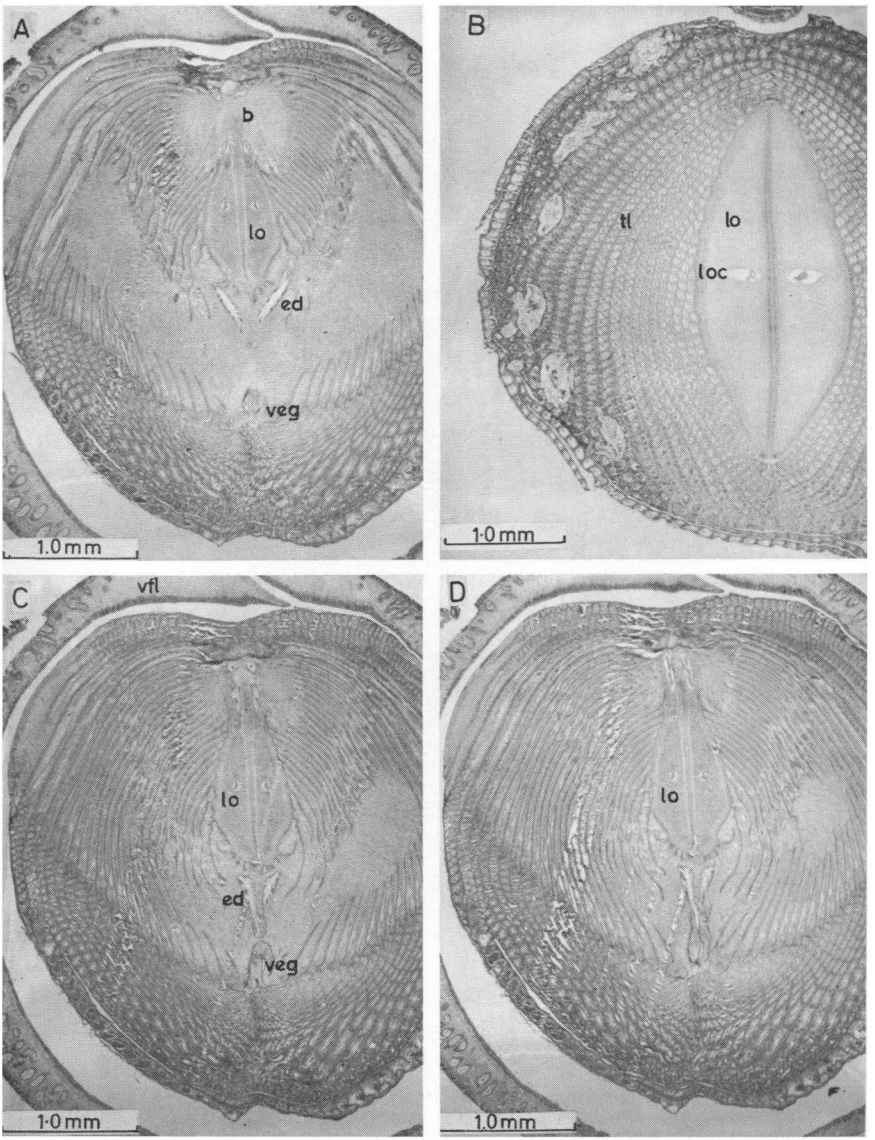

FIGURE 7. A-D, transverse sections through the tentacular crown at various levels: A, C, D, a posterior/anterior series showing the paired lophophoral organ, dorsal to which lies the brain in A. Nerves issuing from the brain and passing to the tentacular lamellae are shown. Ventral to the lophophoral organ are the paired excretory ducts which open (in D) into the ventral groove. B, an illustration of the concentric tentacular lamellae around the paired lophophoral organ. (Sections of copepods can be seen in this section.)

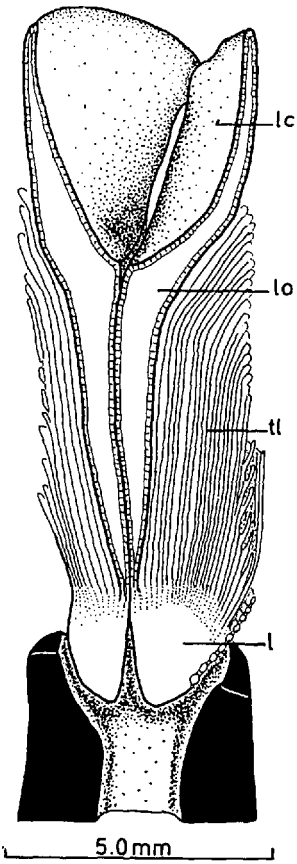

FIGURE 8. A schematic representation of the tentacular crown as seen in a horizontal section, showing the lophophoral cupule and organ around which are arranged the tentacular lamellae.

The halves of the lophophoral organ are identical, and when applied to each other they form a cone-shaped structure with the apex proximal (Figs. 6; 8). Distally each half is built into a deep half-cup-like structure so that when the halves are together they form a deep cup, here called the lophophoral cupule (Fig. 8). In the retracted condition the distal end provides protection for the tentacular lamellae as well as forming a plug to the tube which protects the animal when it is withdrawn into the tube.

It seems possible that such a protective device has evolved in this animal because of its large size and also the large size of the tube's opening, which could very easily give access to predacious animals. Interesting is the

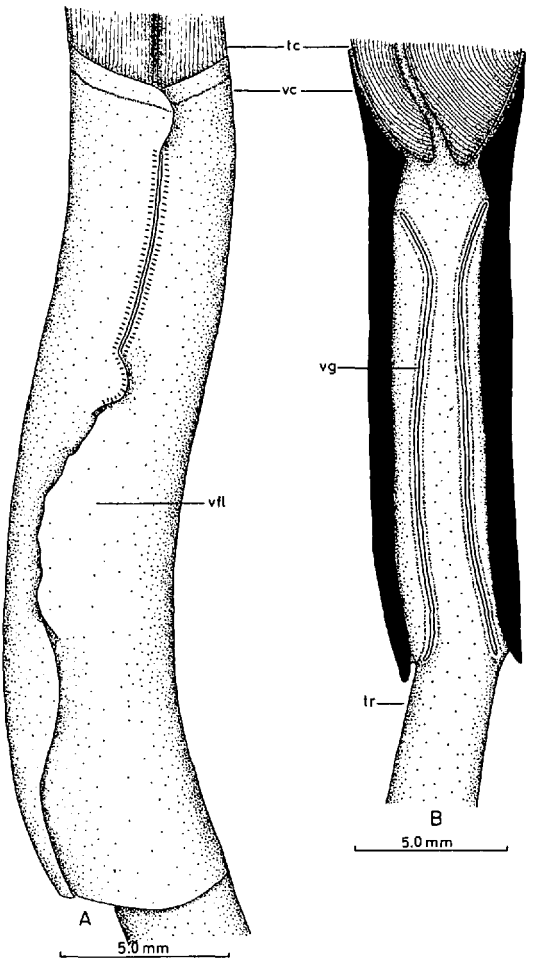

FIGURE 9. A, ventral aspect of the vestimental region with the vestimental folds; B, same, with the folds removed to show the vestimental grooves. (The black areas in B represent the cut surfaces of the vestimental folds.)

presence of as yet unidentified copepods which live in quite large numbers in interlamellar pockets in the tentacular crown (Figs. 6; 7,B). They do not appear to damage the tissue but possibly live as symbionts.

The Vestimental Region.—Measurements of this characteristic region are provided for three specimens in Table 3.

The region is light yellow in colour, and is covered with a honeycomb-patterned superficial layer. Most characteristic are the two lateral body

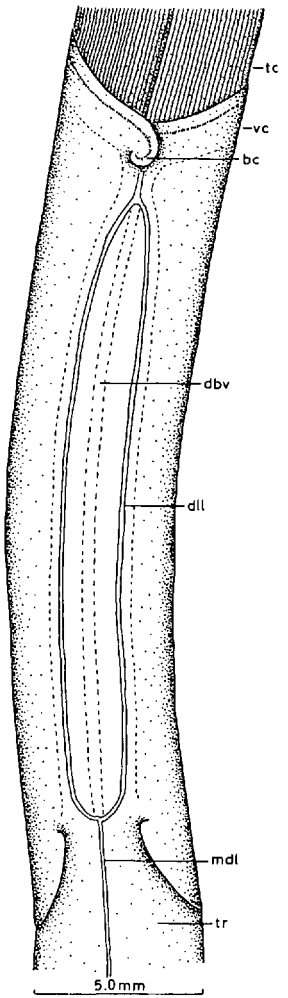

FIGURE 10. Dorsal aspect of the vestimental region.

folds which curve around and meet midventrally, thereby forming a tube, the vestimental tube, which opens anteriorly at the base of the tentacular crown, and posteriorly at the commencement of the trunk (Fig. 9,A,B).

The anterior third of this region (Fig. 9,A) is characterized by possessing, along the margins of the folds, a series of more or less equally spaced darkish lines, which give to this part the appearance of a "zipp." The posterior two-thirds are without such markings.

In one specimen (Fig. 9,A) the folds meet each other midventrally for

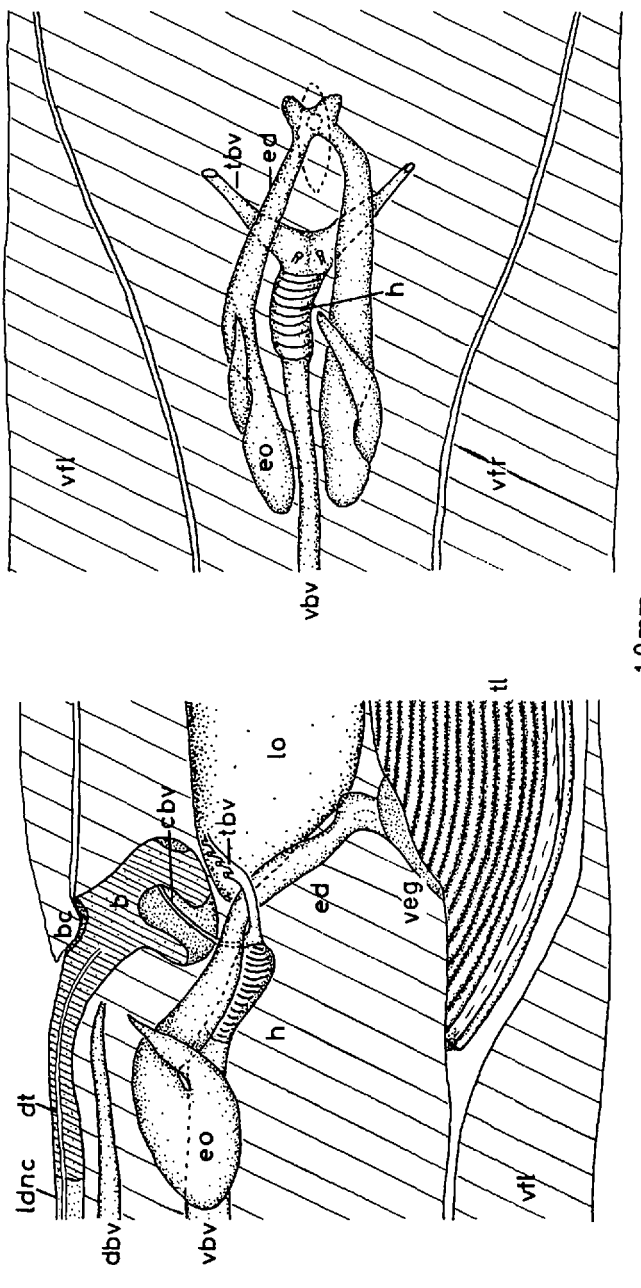

FIGURE 11. *Left*, a median lateral reconstruction of the anterior vestimental region occupied by the excretory organ, its ducts, and the brain; right, a horizontal dorsal reconstruction of the same region. (Oblique lines represent cut surfaces.)

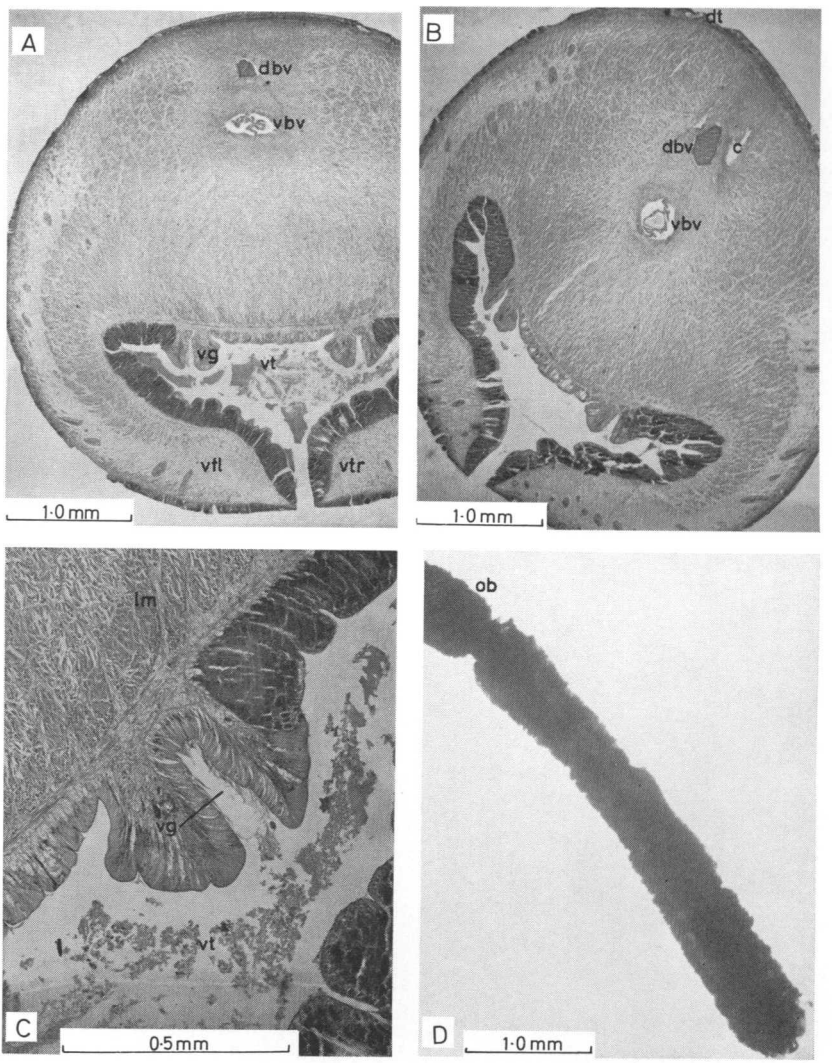

FIGURE 12. A, a transverse section showing the general distribution of structures to be found more or less in the middle of the region; B, a transverse section, considerably posterior to A, illustrating the paired coelomic cavities of the trunk, which extend into the vestimental region and lie on either side of the dorsal blood vessel; C, an enlargement of a portion of a transverse section showing the vestimental groove lined by long cilia; D, the opisthomere.

the first anterior third, thereafter in the second third the left fold overlaps the right, and in the last third the right overlaps the left. In the other two specimens no such overlapping occurs, and the margins of the folds meet in the midventral line throughout the length of the vestimental region.

Anteriorly and dorsally the vestimental region has a small curved flap of tissue (Fig. 10), which is an extension of the collar surrounding the tentacular base. Posterior to this flap is a short, narrow strip of white tissue which is the roof of the brain. The roof has anteriorly a small depression into which fits a thickened portion of the curved median dorsal flap of the vestiment (Fig. 11,A), thereby forming a protective covering to the brain. From the depression arise two parallel dorsal lines which extend posteriorly on either side of the middorsal line. At the posterior end of the vestimental region these two lines join and extend along the middorsal line of the trunk. Between these two lines can be seen, by transparency, the dorsal blood vessel, which disappears from view in the region of the brain and posteriorly where the two parallel lines meet (Fig. 10). The honeycomb pattern is absent between the two lines as well as from a narrow strip on either side of the lines (Fig. 10).

Anteriorly, the vestimental region forms a collar surrounding the base of the tentacular crown. The anterior part of the collar is fairly thin and is externally marked by a thin, dark-brown line (Fig. 10). Ventrally the halves of the collar meet in the midventral line, and dorsally the left overlaps the right with the left part forming the curved structure which forms a protection to the roof of the brain.

Posteriorly, the vestimental region forms an incomplete collar surrounding the anterior end of the trunk laterally and ventrally, where the halves either overlap each other or meet in the midventral line.

On the ventral surface of the vestimental region, covered by the vestimental folds and forming the roof of the vestimental tube, are two pairs of parallel ridges. Between the members of each pair of ridges is a deep groove (Figs. 9,B; 12,A-C). These grooves start a short distance back from the base of the tentacular crown, pass posteriorly as two parallel grooves lying alongside the junctions of the folds and the body proper (Figs. 9,B; 12,A,B), and end just anterior to the start of the trunk. These two grooves are completely protected by the vestimental folds.

In both the male and the female, the paired genital ducts open into the grooves posteriorly.

The Trunk.—The trunk of *Lamellibrachia barhami* is, like that of other Pogonophora, very long. The average length is 354 mm, which is 89 per cent of the total length of the animal. The diameter is more or less uniform throughout the length, being about 4.5 mm at the anterior end, and tapering to about 0.71 mm just anterior to the opisthomere.

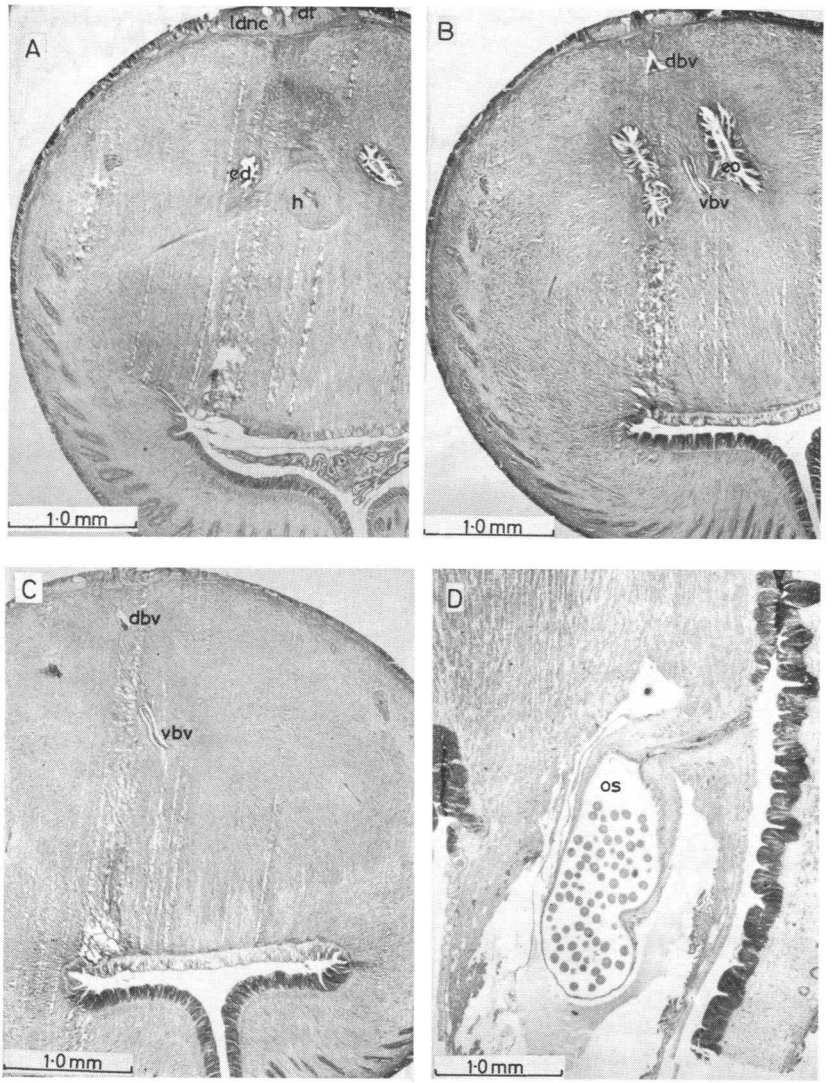

FIGURE 13. A-D, sections through the vestimental region: A, transverse section in the region of the heart and excretory ducts; B, transverse section, just posterior to the heart, showing the excretory organs on either side of the ventral blood vessel; C, a typical transverse section, posterior to the excretory organs and anterior to the commencement of the vestimental grooves; D, a horizontal longitudinal section through the ovisac, with ova, showing its duct leading into the vestimental groove (not clearly shown).

L. barhami is unlike other Pogonophora, because the trunk cannot be subdivided into the characteristic regions designated (preannular, annular, and postannular), each with its own particular subdivisions and features. The trunk is not delimited from the vestimental region by a circular groove.

The Opisthomere.—Figures 4 and 8,D illustrate the opisthomeres of three specimens. Anteriorly, the opisthomere has a prominent bulblike region, which is demarcated from the trunk by a circular constriction. Posterior to the bulb is another constriction, after which is the terminal part of the opisthomere, which is narrow and uniform in diameter. Externally there is no sign of segmentation, nor are there any setae.

The bulb in one specimen has a diameter of 1.10 mm, and in another, 0.83 mm. In the third specimen the bulb is not clearly visible. The diameter of the bulb is greater than the diameter of the trunk immediately preceding it (see Table 3). The diameter of the opisthomere immediately posterior to the bulb is 0.58 mm to 0.90 mm, and the length is between 5.26 mm and 4.2 mm.

Internal Anatomy

The internal anatomy of *Lamellibrachia barhami* has not yet been fully worked out. However, certain aspects of the internal organization are presented in order to substantiate arguments relating to the systematics of the animal.

The Vestimental Region.—The most characteristic feature of the internal organization of this region is the absence of separate paired coelomic cavities such as are found in all other Pogonophora so far studied. Traversing the vestimental region are the dorsal and ventral blood vessels (Figs. 8, A,B; 13,B,C).

On each side of the heart lies one member of a pair of small excretory organs; from the pair of organs a pair of ciliated excretory ducts arises. These two ducts pass anteriorly, and just before they open to the exterior they unite and open by a common excretory pore into a ventral groove at the base of the tentacular crown, which is covered by the bases of the tentacular lamellae when the animal is withdrawn into its tube (Figs. 7, A,C,D; 11,A,B).

It has not been possible to trace the course of the dorsal blood vessel anteriorly and its connection with the vascular system of the tentacular crown and lophophoral organ. The ventral vessel, however, in the region of the excretory tubules, has a very thick wall composed of circular muscle fibres, and a very narrow lumen (Figs. 11,A,B; 13,A). This portion of the ventral vessel forms the heart. Anterior to the heart, paired tentacular vessels arise (Fig. 11,A,B) which provide blood to the tentacular crown and the lophophoral organ. Just before the origin of the tentacular vessels

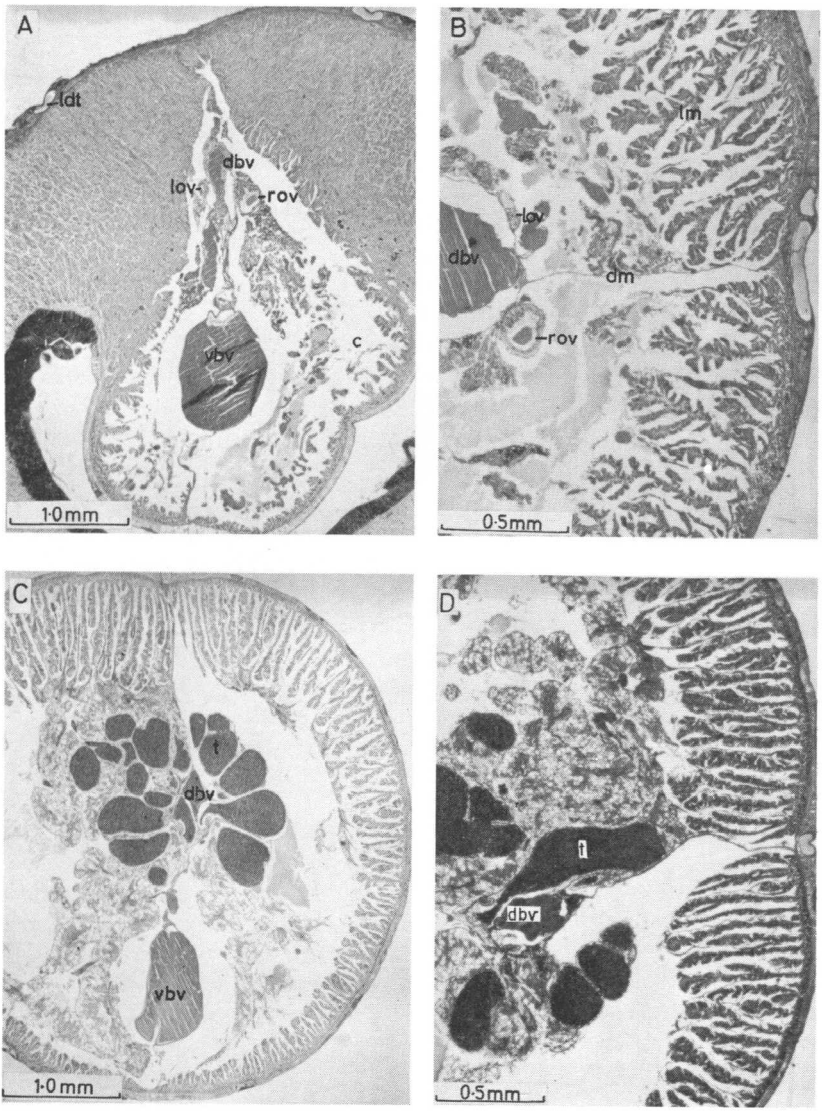

FIGURE 14. A, transverse section through the posterior end of the vestimental region of a female specimen; B, an enlargement of a portion of a transverse section, showing the dorsal part of the trunk of a female; C, a typical transverse section through the trunk of a male; D, an enlargement of a portion of a transverse section, showing the dorsal part of the trunk in a male.

there arises from the dorsal side a pair of small cerebral vessels which enter the brain (Fig. 11,A).

The nature of the coelom within the tentacular crown has not yet been fully worked out. However, all the tentacles are provided with a coelom, as is the lophophoral organ (Figs. 6; 7,A-D). There does not appear to be a connection between the coelom of the tentacular crown and the excretory tubules.

The tissue comprising the substance of the vestimental region is muscular and formed primarily of longitudinal fibres (Figs. 12,A-C; 13,A-D; 14,A). There is only a very narrow circular band of fibres lying beneath the ectoderm which is composed of a single layer of columnar cells. Scattered in a subepidermal zone of the vestimental folds and on the lateral sides of the vestimental region are numerous multicellular glands, each of which opens to the exterior by a small pore (Figs. 12,A,B; 13,A-C).

Anteriorly and lying dorsal to and just in front of the heart is a well-developed brain (Figs. 7,A,C; 11,A). The brain is continuous with a short intraepidermal nerve cord which soon divides into paired dorsal nerve cords (Figs. 11,A; 13,A-C) extending the full length of the vestimental region, at the posterior end of which they unite and form the intraepidermal nerve cord of the trunk (Fig. 14,C,D). Lying intimately associated with the nervous system is a pair of dorsal tubes which are represented externally by lines. These tubes (Figs. 11,A; 12,A,B; 13,A-C; 14,A,B) pass anteriorly and enter the substance of the brain as very fine tubules. Posteriorly they follow the same course as the nerve cords. Arising on either side of the brain are nerves which go to the bases of the tentacular lamellae (Fig. 7,A,C,D).

The deep vestimental grooves are bounded by tall ridges formed from very tall columnar epithelial cells, the distal ends of which bear very long cilia (Fig. 12,C).

The Trunk.—The trunk is traversed by the dorsal and ventral blood vessels, of which the ventral is by far the larger (Fig. 14,C). These vessels are supported by dorsal and ventral mesenteries that divide the coelom into two cavities, which extend the full length of the trunk. These coelomic cavities extend into the posterior third of the vestimental region (Figs. 12,B; 14,A,C). There is no sign of a transverse muscular diaphragm dividing the coelomic cavities of the trunk from their extensions into the vestimental region.

Middorsally and extending the full length of the trunk is the intraepidermal dorsal nerve cord with its associated dorsal tube, which is covered in the middorsal line by a thin layer of cuticle (Fig. 14,C,D).

The muscular layers lying beneath the single-layered epidermis are formed of a narrow band of circular fibres followed by a thick layer of

longitudinal fibres very similar to the longitudinal musculature of the earthworms. Dorsally and laterally the longitudinal musculature is broad, while ventrally it is considerably narrower (Fig. 14,C).

Throughout the trunk are numerous scattered multicellular subepidermal glands which are to be found in the longitudinal muscle layer and which open to the exterior by small pores. These glands and those of the vestimental region possibly produce the tube-forming material. Also to be found are small, scattered, cuticular plaques which project only very slightly above the general body surface.

The Reproductive Organs.—The sexes are separate and externally they are indistinguishable. In the male the testes are multiple lobate structures occupying most of the trunk, and they project into the coelomic cavities (Fig. 14,C,D). The vasa deferentia extend anteriorly into the posterior end of the vestimental region where they open into the posterior ends of the paired vestimental grooves. Though the two male specimens studied appear to be sexually mature, spermatophores of the pogonophoran type have not been seen.

In the single female studied, the reproductive system is simple. The ovaries are simple, paired, tubular structures extending some distance into the trunk and lying in close proximity to the dorsal blood vessel in a dorsolateral position (Fig. 14,B). Further anteriorly in the trunk, and in the posterior end of the vestimental region, the ovaries lie lateral to the dorsal blood vessel (Fig. 14,A). In this specimen only the right ovary and right genital duct appear to be functional, the left ones being very small and difficult to distinguish.

The ovary of the right side as it passes anteriorly gradually increases in size and forms the oviduct. The oviduct is lined with ciliated epithelial cells, and the lumen is filled with eggs. Anteriorly the oviduct narrows slightly and then opens into a large saclike structure, the ovisac, which in turn opens to the exterior at the posterior end of the vestimental groove of that side (Fig. 13,D).

Discussion

Lamellibrachia barhami, gen. nov., sp. nov., is unique. The generic name reflects the character of the tentacular crown in which the tentacles are fused to form concentric horseshoe-shaped lamellae around a central paired lophophoral organ. The only other known pogonophores having fused tentacles belong to the families Lamellisabellidae and Spirobrachiidae of which the latter family is "distinguished from all other Pogonophora by the development of a lophophore—a peculiar unpaired outgrowth of the protosoma bearing the major part of the tentacles" (Ivanov, 1963:13). The specific name *barhami* is in honour of Dr. Eric Barham, who very kindly consented to have this animal named after him.

There is little doubt that *L. barhami* is a pogonophore. Its inclusion in the phylum is based primarily on the shape, structure, and protein content of the tube. The details of the protein analysis will be published shortly. The animal has only three features that show distinctive pogonophoran characters: the very long trunk region, the metasoma, and the absence of a gut.

The metasoma is possibly the only positive pogonophoran characteristic. Webb (1964a, b, d) described what he called "the anchor" in *Siboglinum fiordicum, S. ekmani,* and *Sclerolinum brattstromi.* Ivanov (1964) described this body region in *Siboglinum caulleryi,* and Bubko (1965) described such a body region in *Choanophorus indicus.* In the three species of *Siboglinum* and in *Choanophorus* the metasoma has setae, while setae are absent in *Sclerolinum* and in *Lamellibrachia barhami.* Another feature of the metasoma is the presence of a bulbous region which precedes the setigerous region. This bulbous region is absent in *Sclerolinum brattstromi* and *Choanophorus indicus,* and it has not been described in *Siboglinum caulleryi.*

The distinctive pogonophoran body region is the metasoma (Webb, 1964a-e, 1965), a view that has recently been confirmed by Southward & Southward (1966). There is little doubt that the metasoma of *Lamellibrachia barhami* is homologous with the metasoma of the three abovementioned species of *Siboglinum,* the single species of *Choanophorus,* and *Sclerolinum brattstromi.* It has previously been suggested that the metasoma will possibly be found in all Pogonophora (Webb, 1964a).

Phyletic characters, as given by Ivanov (1952, 1954, 1955, 1956, 1957, 1959a, 1963), Southward (1963), Hyman (1959), and others, cannot be rigidly applied to *Lamellibrachia barhami.* Despite this, I have no hesitation in assigning this species to the phylum Pogonophora.

Ivanov (1955, 1957, 1963) divided the Pogonophora into two orders, the Athecanephria and the Thecanephria. Nielsen (1965) has given a full discussion of these two orders and concludes that "only the internal anatomy of the forebody can give a fully reliable distinction" (*op. cit.,* p. 985).

The distinction between the two orders lies in the morphology of the excretory organs. In the Athecanephria the "coelomoducts are wide apart with their excretory sections closely adjoining the lateral cephalic vessels" (Ivanov, 1963:154). In the Thecanephria "the excretory sections of the coelomoducts of the protosoma approach the boundary of the metasoma [*sic*] in the median plane, where they lie in sac-shaped extensions of the dorsal blood vessel" (Ivanov, 1963:331).

Using the above criteria as a means of distinguishing the two pogonophoran orders, *Lamellibrachia barhami* cannot be included in either on the grounds that the paired excretory organs show no connection with the coelom of the tentacular crown and lophophoral organ, and that the ducts

are undifferentiated and lie lateral to the ventral blood vessel and the heart. The ducts join, forming a common excretory pore which opens into a ventral groove lying at the base of the tentacular crown.

The other characters distinguishing the Athecanephria and the Thecanephria are not altogether reliable (Nielsen, 1965). The presence of fused tentacles, and a tube with a hard, funnel-like anterior end cannot be used as an argument for including this species in the Thecanephria. Other characters used by Ivanov (1963), e.g., the postannular region and the spermatophores, likewise cannot be used because of the absence of a postannular region in *L. barhami* as well as the absence of typical pogonophoran spermatophores.

There is little doubt that *L. barhami* cannot be assigned to either of the two existing pogonophoran orders. Therefore, it is proposed to place this species in a new order, the Vestimentifera. In establishing a new order it becomes necessary to look for distinctive characters which differ sufficiently from existing ordinal characters to justify the erection of a new order. The characters of the order **Vestimentifera,** ord. nov., are:

1. Simple paired excretory ducts without connections with the tentacular coelom; the ducts open to the exterior by way of a single median excretory pore that finds its opening in a ventral groove situated at the base of the tentacular crown and which is completely covered by the tentacular lamellae when the animal is retracted into the tube.
2. The trunk is undifferentiated along its entire length, but is provided with numerous small and scattered papillae. There are also numerous small cuticular plaques scattered over the entire surface.
3. The tentacular crown is formed from numerous fused tentacles forming concentric horseshoe-shaped lamellae surrounding a paired, centrally placed lophophoral organ.
4. The second body region, the vestimental region, has lateral body folds that meet in the midventral line to form a vestimental tube, on the dorsal side of which are paired ciliated grooves.
5. The male and female external genital apertures open into the vestimental grooves posteriorly.

At this stage, the new order contains but a single family, the **Lamellibrachiidae,** fam. nov., with the characters of the order.

Attention must now be given to other morphological and anatomical characteristics of *L. barhami* which are both distinctive and unique when compared with the phylum as a whole.

Apart from the previously mentioned phyletic characteristics, that of the tube, the absence of a gut, and now the inclusion of the metasoma, the phylum is defined as having a trisegmental body composed of: the protosoma with a tentacular apparatus and cephalic lobe and with a single

coelom; a mesosoma with paired coelomic cavities and with a bridle; and a long metasoma (*sic*) divided into regions and with paired coelomic cavities. As previously mentioned, the body regionation, as defined by Ivanov (e.g., 1963), is not acceptable. The mesosoma is the longest part of the body and is secondarily divided into an anterior part with a bridle, and a long trunk part which is regionated. The metasoma is restricted to a small multisegmental opisthomere, with or without setae.

Having established the adult pogonophoran body regions, it is now possible to put forward certain proposals concerning the classification of the phylum, taking into account the distinctive characteristics of *L. barhami.*

Lamellibrachia barhami clearly shows basic differences from other members of the phylum. These differences are as follows: the cephalic lobe of the protosoma is absent; the bridle of the first mesosomal segment is wanting; the first segment of the mesosoma has ventrolateral folds, which are absent in all other pogonophorans; the trunk is undifferentiated into the characteristic regions; there is no ciliation of the trunk in *L. barhami,* such as is to be found in all other Pogonophora on the dorsal side of the metameric region of the second mesosomal segment; there are no toothed platelets.

The internal organization of *L. barhami* is very different from that of those species which have been investigated in both orders. The external openings of the genital ducts in *L. barhami* open into the posterior end of the vestimental grooves, whereas in the other Pogonophora the male openings are to be found at the extreme anterior end of the trunk, and the female openings are about halfway along the trunk, but anterior to the girdles of toothed platelets. There is no muscular diaphragm and corresponding external constriction between the first and second mesosomal segments. An external constriction is wanting in *Sclerolinum sibogae* (Southward, 1961b) and *S. brattstromi* (Webb, 1964f).

In the already described Pogonophora there is a brain, situated in the protosoma, from which arises a single intraepidermal nerve cord extending along the length of the animal (Ivanov, 1959b, 1963). In *Lamellibrachia barhami* the large brain lies just posterior to the tentacular crown and slightly anterior to the heart (Fig. 11,A). From the brain there issues a single intraepidermal nerve cord which very soon divides into two single nerve cords extending the length of the vestimental region, at the posterior end of which the two nerve cords join and form a single intraepidermal dorsal nerve cord which extends the full length of the trunk. Associated with the brain and the nerve cords are the dorsal tubes. The nervous system, including the dorsal tubes, shows very little similarity with that of other pogonophores other than being dorsal in position and intraepidermal.

The coelomic cavities of *Lamellibrachia barhami* are also different from those of other Pogonophora. The general pattern of the coelomic cavities

in the Pogonophora is as follows: there is a single protocoel which opens to the exterior by way of a pair of excretory ducts; in the second segment there is a pair of coelomic cavities without coelomoducts; and in the third segment, or trunk, there is also a pair of coelomic cavities with coelomoducts functioning as gonoducts. In this new species the tentacles and lophophoral organ have coelomic spaces, but there is no obvious single coelomic cavity, and there is no apparent junction between the coelomic spaces of the tentacular crown and the excretory organs. The vestimental region has, for most of its length, no coelomic cavities; however, the paired coelomic cavities of the trunk extend into the posterior third of the vestimental region and terminate blindly on either side of the dorsal blood vessel. The paired coelomic cavities of the trunk extend its full length and terminate blindly just anterior to the start of the opisthomere. The condition of the coelomic cavities of the opisthomere has not yet been investigated.

Because of all these differences, fundamental to the organization of the Pogonophora, and of many others which will be dealt with in future papers, it is obvious that *Lamellibrachia barhami* stands alone in the phylum. For this reason it is suggested that two classes be erected to satisfy these distinguishing features of *Lamellibrachia barhami.* The two classes proposed are: **Afrenulata,** class nov., which includes the single species *Lamellibrachia barhami* because it lacks a bridle (or frenulum), and the **Frenulata,** class nov., which includes all the other known pogonophores because they each possess a bridle.

The presence or absence of a mesosomal bridle has been selected as the all important character used to distinguish these two classes of Pogonophora because it is the bridle that plays the very important role in formation of the tube (Webb, 1965). The afrenulate pogonophores cannot form the tube in the manner suggested for the other members of the phylum. However, in these forms the whole of the vestimental region is the tool by means of which the tube-forming material can be spread layer upon layer and also the means by which the tube is lengthened.

The formation of the vestimental folds has possibly developed for two reasons. The first reason is possibly that of providing this region with an adequate surface area so that the tube-forming material can be evenly spread and also as a means of enlarging the vestimental region in diameter by contraction of the longitudinal musculature so that the body fits firmly into the tube. The second reason is possibly associated with embryonic development. As the sperms and eggs are shed into the vestimental tube at the posterior end of the vestimental grooves it means that they can be transferred to the front of the animal without damage.

It should be emphasized that the classification of the Pogonophora should undergo a revision in the light of new information, particularly now that

we know that the pogonophoran body does not consist of only three segments.

Summary of New Taxa

Class Frenulata, class nov.

Includes all pogonophorans with a frenulum (bridle).

Class Afrenulata, class nov.

Includes pogonophorans lacking a frenulum (only one species so far discovered).

Order Vestimentifera, ord. nov.

With the characters enumerated on page 42. Contains only a single family, as follows:

Family Lamellibrachiidae, fam. nov.

With the characters of the order. Type genus, *Lamellibrachia,* gen. nov., containing a single species, *Lamellibrachia barhami,* sp. nov., which is here designated as the type-species.

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Sumario

Lamellibrachia barhami Nov. Gen., Nov. Sp. (Pogonophora) del Pacifico Nororiental

Lamellibrachia barhami nov. gen., nov. sp., es un pogonóforo singular que ha sido asignado a una nueva clase, Afrenulata nov. clase, un nuevo orden, Vestimentifera nov. orden y a una nueva familia, Lamellibrachiidae nov. fam. Todos los pogonóforos previamente descritos han sido incluídos en una nueva clase, Frenulata nov. clase. La distinción fundamental entre las dos clases descansa en la presencia o ausencia de una brida (frenulum).

L. barhami tiene un diámetro tres veces el tamaño del mayor pogonóforo descrito. La corona tentacular comprende unos 25 tentáculos laminares dispuestos concéntricamente alrededor de un órgano lofoforal par. No tiene lóbulo cefálico, típico de todos los otros pogonóforos. La segunda

región, "región vestimental," no tiene freno. En ella se presentan dobleces pares del cuerpo que se hallan en la parte media ventral y circundan un tubo vestimental, en el lado dorsal del cual hay un par de surcos ciliados, los surcos vestimentales. El tronco no está separado de la región que le precede por una hendidura circular, ni está separado en regiones como en otros pogonóforos. El par de órganos excretores abre al exterior por un solo poro excretor medio dentro de un surco ventral en la base de la corona tentacular. Los sexos están separados y los conductos genitales abren en los extremos posteriores de los surcos vestimentales. Asociados con el cerebro y los cordones nerviosos intraepidermales hay un tubo dorsal.

En la región vestimental hay pares de cordones nerviosos intraepidermales que se unen y forman un cordón nervioso intraepidermal dorsal único de la región del tronco. La región vestimental no tiene cavidades celómicas independientes. Las cavidades celómicas pares del tronco se extienden hasta el extremo posterior de la región vestimental.

El cuerpo termina en un opistomero que es el metasoma y el cual es homólogo con el metasoma de tres especies de *Siboglinum,* una especie de *Sclerolinum* y la única especie de *Choanophorus.*

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